

BEHAVIOR, LIFE CYCLE AND WEBS OF *MECICOBOTHRIUM THORELLI* (ARANEAE, MYGALOMORPHAE, MECICOBOTHRIIDAE)

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ABSTRACT. A comprehensive study of the biology of *Mecicobothrium thorelli* Holmberg 1882 was carried out in the laboratory and in the field (Sierra de Animas, Maldonado, Uruguay). The species is found in shady riparian sites under trees. *M. thorelli* builds sheet-and-funnel webs under stones, logs, roots and in crevices. In the laboratory, developmental data indicated that the spiders have an inactive phase in summer and probably another in winter. Adults emerged in the fall and the males die during late winter. Three egg-clutches of about 30 eggs were observed in the laboratory at the end of winter and the beginning of spring (August–September). Juveniles emerged from one of the clutches 27 days after oviposition. A three-year lifespan was estimated. Males started courtship (body vibrations and palpal drumming) upon contacting the female web. Females showed high tolerance during the entire sexual interaction. An unusual clasping mechanism was observed before and during copulation: the female engaged her cheliceral fangs into grooves on the male chelicerae. Twenty-eight copulations were observed. Mean copulation duration was 24.7 min, while males performed a mean of 10 alternate palpal insertions. The complex insertion pattern is described and analyzed. Half of the copulated males pursued females after uncoupling. These males expelled females from the web and remained there. Mated males aggressively defended the female's web from other males. The reproductive strategy, cheliceral clasping and palpal insertion pattern are discussed in detail. Phylogeny and biogeography of mecicobothriid genera are also considered.

The family Mecicobothriidae was established by Holmberg (1882) to include small-sized mygalomorphs found in Argentina. These spiders have unique morphological features (abdominal tergal plates, longitudinal fovea and elongated posterior lateral spinnerets). Mecicobothriid monophyly was supported by Gertsch & Platnick (1979) and by Raven (1985). Recently, Goloboff (1993) placed Mecicobothriidae as a sister group of the non-atypoid Mygalomorphae. Following Barrowclough (1992) this characteristic justifies giving high priority to the conservation of the Mecicobothriidae, considering the importance of this family to studies of spider phylogeny. The geographic distribution is also crucial because these spiders are only known from temperate regions of North and South America.

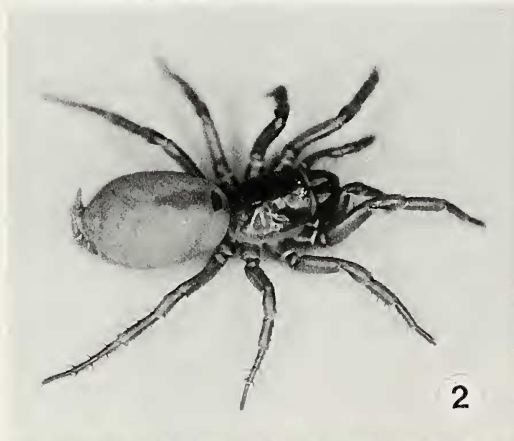
Mecicobothrium thorelli Holmberg 1882 (Figs. 1, 2) is the only mecicobothriid known from the Southern Hemisphere. It was originally recorded from Argentina (Buenos Aires: Tandil, Balcarce and Sierra de la Ventana (Gertsch & Platnick 1979)) and Uruguay

(Maldonado, Sierra de las Animas (Capocasa et al. 1989)). Other Mecicobothriidae occur only in North America. Biological data on North American mecicobothriid species were given by Gertsch & Platnick (1979). *M. thorelli* was found in Uruguay in hilly zones in riparian woods under stones, roots and trunks, and in holes in the tree bases (Costa et al. 1991; Pérez-Miles et al. 1993). Lack of knowledge of the biology of this group, together with the presence of enigmatic cheliceral male apophyses, challenged us to conduct field and laboratory studies on the biology of *M. thorelli*.

Our objective was to describe and analyze the development, life cycle, phenology, webs and, especially, the sexual behavior of *M. thorelli*. This last aspect, poorly known in Mygalomorphae, is unknown in Mecicobothriidae.

METHODS

Specimens of *M. thorelli* were collected at Sierra de las Animas, Maldonado, Uruguay, in



Figures 1–3.—*Mecicobothrium thorelli*. 1, Adult male; 2, Adult female; 3, Sheet and entrances of *M. thorelli* web in the laboratory. (Photos by M. Lalinde).

the streamside forest of Pedregoso Stream (34°45'S, 55°15'W). The cryptozoic arachnofauna of this site has been intensely studied (Capocasale et al. 1989; Costa et al. 1991; Pérez-Miles et al. 1993; Capocasale & Gudynas 1993; Costa & Pérez-Miles 1994). Voucher specimens were deposited in the arachnological collection of the Museo Nacional de Historia Natural, Montevideo.

Six field collections were made: 1) 4 females, 2 males and 5 juveniles on 29 June 1989; 2) 1 female and 9 juveniles on 16 August 1989; 3) 3 juveniles on 20 November 1989; 4) 3 females, 1 male, 5 juveniles on 18/19 May 1990; 5) 33 juveniles on 9 September 1994; and 6) 36 juveniles on 21 September 1995. Individuals from the last collection were measured and released, except six which were raised. Silk constructions were observed in the field. On 30 June 1993, measurements were made of 17 webs of *M. thorelli*, the stones that covered them, and the distances to the stream (spiders were not collected).

Seventy-two individuals were kept in the laboratory from June 1989–April 1996. Most individuals were placed in glass vials of 80 mm × 15 mm, with damp cotton wool at the bottom end and dry cotton wool closing the open end, leaving 5 cm of free space in the vial for the spider. Vials were maintained slightly inclined with the open end upward. For specific observations and for short periods spiders were maintained in: a) glass jars of 9 cm diameter, with soil, water provision and a microslide covered with a plumb bob. Under the microslide we made a small burrow to facilitate spider excavation. Plumb bob removal allowed us to observe the spider. b) Arena A. Petri dishes of 9 cm diameter with a damp cotton wool placed centrally and a small vial (30 mm × 7 mm) with both ends open, placed against the dish wall. c) Arena B. Cylindrical glass jars of 14 cm diameter, with soil, water and a piece of wood of 3 cm diameter placed on the soil. We made a small burrow under the wood to facilitate spider excavation.

The temperature in the laboratory varied with the outdoor temperature, except in winter when it was maintained around 20 °C (range: 15–23 °C). Natural light was provided by windows facing west; artificial light was on from Monday to Friday from 0830 to 1700 h. Spiders were fed mainly with *Tenebrio* sp. larvae

(alive or in pieces), sometimes complemented by flies, mosquitoes, small beetles, silverfish, etc.

Thirty male-female encounters were set up with 32 of the spiders collected on 9 September 1994. Twenty observations of these encounters occurred in a female breeding vial connected to an open petri dish (9 cm diameter), containing sand and surrounded with a plastic band 45 mm high (Arena C). The entrance (2 cm) of the female's glass tube had no silk because the cotton wool plug was removed before the encounter. Arena C was elevated in such a way that observations could be made from below using a 5 \times lens and focused light. Six observations were done in Arena A and the other four in Arena B. All available males and females were used. Observations were carried out between 9 May–3 July 1995 (fall/winter). Laboratory temperature varied between 16 and 24 °C; observations were conducted at 22.2 ± 1.1 °C (range: 19–23.5 °C). Other male-female encounters, including a copulation, were recorded on Super-8 movie film.

RESULTS

Webs and retreats.—The spiders construct dense funnel-and-sheet webs (see Coyle's 1986a nomenclature). The web, after experimental wetting, appeared to be hydrophobic. The distance from the web to stream edge for seven individuals was 5.28 ± 4.55 m (range 0.57–10 m). The web nearest the stream was found at 25 cm above the water level. Presumably the spiders remain in the retreats during short-term rain-caused flooding. In the laboratory, we observed that they easily drown in a fine water film if webs are lacking. Two of 17 webs observed in the field were not occupied; no male was observed occupying a complete web.

The funnel (tubular retreat) of the web extends under the stone (or similar object) and emerges with one or more entrances onto a small, irregular prey capture sheet (Fig. 3). In the field, this sheet lies on the soil, extends to both sides of the entrances, and continues beneath the leaf litter, moss or grass. Retreat tubes were more or less curved, some of them branched. Seven webs had only one entrance, two webs had three entrances, and one had four entrances. Eight webs were found under stones and one was under a log. Stones with

webs measured 225 ± 101 mm long, 168 ± 59 mm wide and 103 ± 33 mm high. The mean major axis of the silk tubes was 64 ± 20 mm and their diameter varied from 4–8 mm. A web constructed in the laboratory by an adult female consisted of two more-or-less parallel tubes fused medially (H-shaped web): its total length was 23 mm, the exposed portion lying on the soil was 14 mm, and the underground portion was 9 mm. This web was constructed under a small section of a branch placed on the soil.

Females which copulated in the laboratory and lived in glass vials exhibited reduced web construction in winter. Eight females placed in containers with soil each occupied a burrow made for it under a piece of glass. These females did not make webs but excavated and closed the burrow entrance with soil and silk. Usually males made a silk mat in the glass vials during winter, but only one male made a rudimentary retreat. Males placed in containers with soil similar to those used for females rarely occupied pre-existing burrows.

Prey capture.—When a prey is offered, the spider detects vibrations through the web and suddenly approaches the prey, biting it and pulling it back to the retreat, entangling the prey with silk threads while it is being carried. Adult males also fed actively.

Daily activity pattern.—Spiders in the laboratory showed little diurnal activity. When a light was turned on in the dark winter mornings, spiders ran back into their retreats. The dense draglines observed around the inner periphery of the containers suggested they were very active during night.

Development and reproduction.—Thirty-three large juveniles were captured on 9 September 1994. No subadult individuals were found then. The spiders constructed the retreat in the damp end of the glass vial; each retreat had two lateral entrances. One animal died 29 days after capture. The 32 remaining individuals matured in the laboratory (19♂ 13♀). Seasonal distribution of the molts is given in Fig. 4. These spiders molted synchronously at the beginning of October. Between October and December they molted an average of 1.5 ± 0.6 times. Smaller animals molted more frequently than larger ones. In the warm period (last three weeks of January and first two of February) no molting occurred. Molting resumed at the end of February and continued

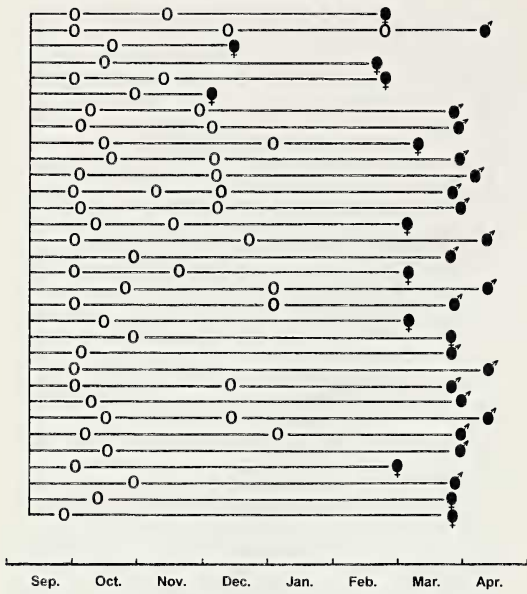


Figure 4.—Development of 32 juveniles collected on September 9, 1994. Empty circles (○) indicate ordinary molts and dark circles (●) indicate the maturation molt and sex.

to April, when all individuals had reached maturity. The spiders carried the exuviae far away from the retreat.

Male palpal tarsi were incrassate in the penultimate instar. No evidence of spermathecae was observed in the last exuviae of females. Females molted over a longer period (December–March) and earlier than the males. Males

reached maturity in a very limited period (last week of March and first two weeks of April) (Fig. 4). The time of maturation molts of both sexes overlapped only in the last week of March. Laboratory rearing showed that males molted (2.79 ± 0.63 times) more times than did the females (2.38 ± 0.51 times), with significant differences in the Mann-Whitney's U -test ($U = 77.5$, $P < 0.05$).

Adults mated in the laboratory from 9 May–3 July 1995. Two males died accidentally (bad manipulation) after the copulation. Males lived 118–206 days ($\bar{x} = 166.5 \pm 22.9$ days, $n = 16$) and females lived 161–298 days ($\bar{x} = 215.5 \pm 41.4$ days, $n = 12$) after reaching adulthood. The male and female adult life-spans were significantly different (Student's t -test; $t = 3.84$; $P < 0.001$).

Complementary results were obtained from five other groups that were reared between 1989–1996 and kept under conditions similar to the previous described group. Molts started in August and were especially frequent in September–December and March–April (Fig. 5). Molts were very rare or absent in June–July and January–February. Maturity molts were frequent in March and April. Two exceptional maturity molts were observed, an early male (February) and a late male (May, dead when molting). Six males raised in the laboratory lived 172.2 ± 19.7 days after maturity. Another male captured as adult lived 160 days. Two females molted in March and lived as adults 206 and 393 days, respectively.

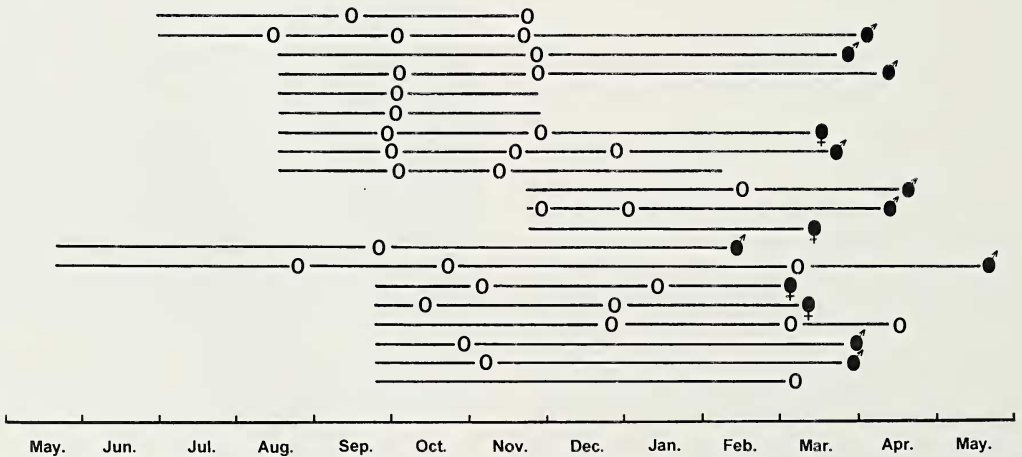


Figure 5.—Development of five groups of *M. thorelli* from five collections. Empty circles (○) indicate ordinary molts and dark circles (●) indicate the maturation molt and sex. Some of these juveniles did not reach maturity due to natural or accidental death, or were sacrificed.

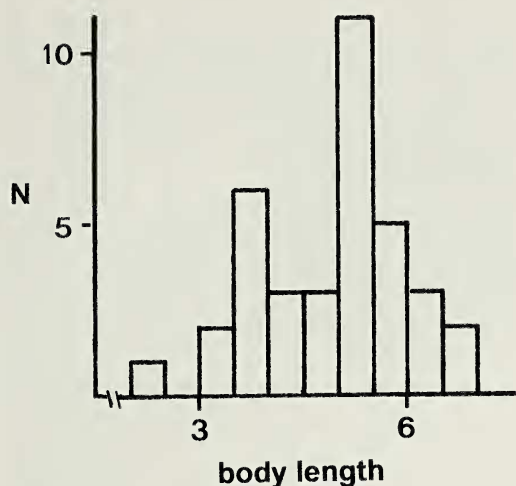


Figure 6.—Body length (in mm) distribution of a sample of 36 individuals of *M. thorelli* collected on 21 September 1995 in Sierra de las Animas, Maldonado. Class intervals: 0.5 mm, N: absolute frequencies.

On 21 September 1995, 36 individuals (no adults or subadults) were captured, and most of them were released after being measured. Six were reared in the laboratory. Measurements of these six were made from successive molts. Body size distribution is shown in Fig. 6. Carapace length increased between 9.4 and 22.0% during the molt ($\bar{x} = 15.5 \pm 3.4\%$, $n = 14$). The relative size increase was not related to the size of the individual. Small spiders (less than 3 mm body length) are very light brown while large juveniles are darker. The abdomen of some adult females becomes lighter when swollen.

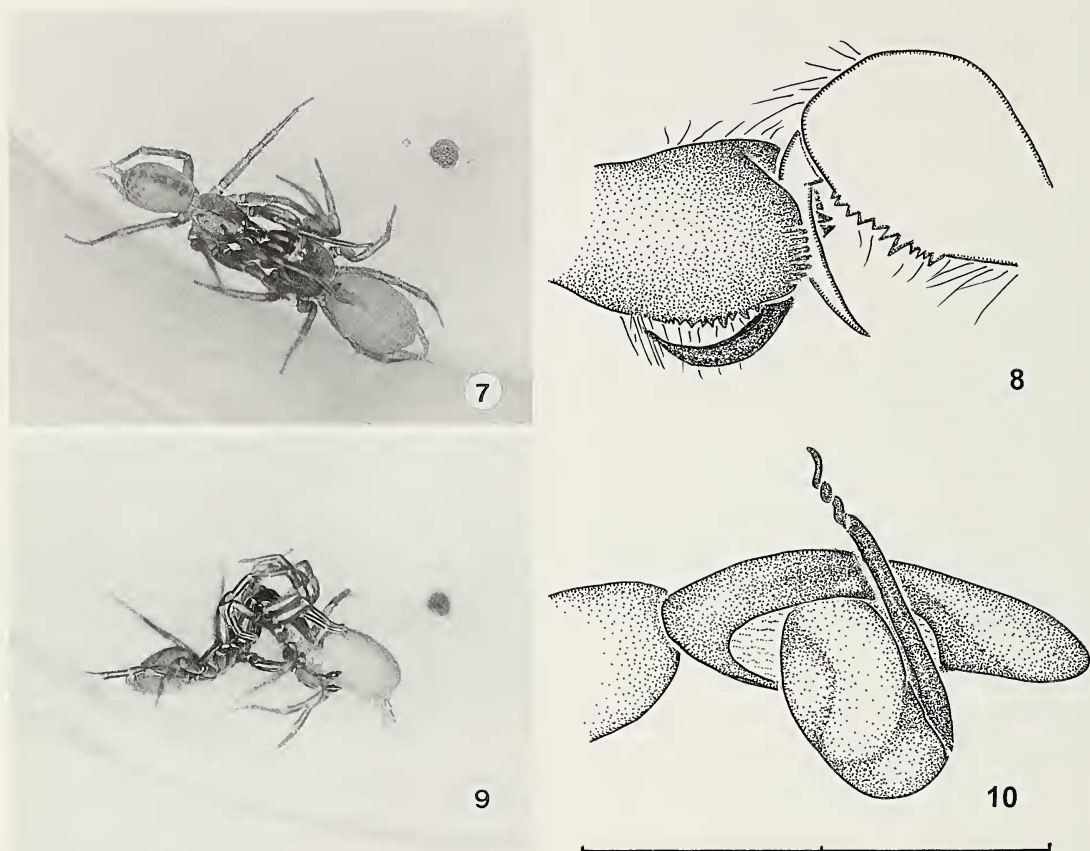
In the laboratory males had their maturation molt between February and May, with a clear peak between March and April (Figs. 4, 5). Adult males lived from February to October. An egg-clutch was observed in the laboratory on 27 September 1989, from a female collected on 16 August. In the retreat, the eggs were agglomerated in a sphere without a well-developed silk cover, resembling the egg-sac of *Pholcus phalangioides* (Fuesslin 1775). The egg-sac, slightly larger than the carapace of the female, contained 33 yellow, translucent eggs. The female kept the egg-sac until the emergence of the spiderlings, 27 days after oviposition. The female died on 9 January 1990. Two other egg-sacs were observed in the laboratory on 31 August: one of them was

eaten immediately by the female, the other contained 26 eggs (all of which were dead and decomposed) when the female died.

Courtship.—In Arena C, males were placed on clean sand and they walked to enter the female's glass vial. A rim of female silk was observed when the cotton plug was removed. Thirteen of 20 males stopped on the silk rim, remained immobile between 4–128 sec, and then started sexual activity. The other seven males began sexual activity just inside the female's web. In Arena B, males walked around the periphery of the arena (on female draglines) but initiated their sexual behavior only very close to the female's retreat. Finally, in Arena A, sexual behavior started close to the small glass vial where the female resided, or after female contact.

Male sexual behavioral units elicited by the female web were: 1) Body vibrations, which are brief, rapid, sagittally orientated body movements, and are apparently caused by leg-III movements. 2) Palpal drumming, which are alternate movements of palps against the substratum; these movements turn into steps when the male walks. 3) Leg tapping, in which the forelegs touch the female's silk mat, pulling the silk and sometimes penetrating it. These units took place alone or during slow locomotion movements and were interrupted by brief motionless periods. The main behavioral sequence was locomotion with body vibrations at the beginning, with leg tapping and palpal drumming added later. Similar behavior was observed in eight males which contacted the silk of females which had been removed from their breeding containers. This first searching phase lasted from 17 seconds to 22 minutes, until the female was contacted. Females did not attack or approach the males but remained immobile or retreated. After making direct contact, the male increased his tapping movements on the female body and legs. The male penetrated the silk and oriented toward the female chelicerae. Then the male pushed the female with his chelicerae. His cephalic region was directed downward while pushing her and his legs I and II held the female, preventing upward biting (Fig. 7). The male exerted a great effort to maintain this frontal position with respect to the female. Females were passive and generally flexed their legs against their bodies.

Males pursued females sometimes with ap-



Figures 7-10.—Copulation in *Mecicobothrium thorelli*. 7, Initial stage of copulation. Male (at left) pushing female with his chelicerae while legs I and II prevent upward biting; 8, Schematic representation of the cheliceral clasping, prolateral view. Female fang (to the right) penetrates into the male cheliceral groove delimited by two apophyses and several cusps; 9, Copulation and palpal insertion. Cheliceral clasping and legs I and II of the male (at left) firmly maintain this position. The long palps of the male are able to reach the female genital zone without extreme elevation of the couple; 10, Embolus position during insertion attempt of male right palp, reproduced from a preserved specimen. (Photos M. Lalinde)

parent violence. The male usually spread apart his chelicerae when pushing the female, but he never attempted to bite her. This sequence was repeated until the female finally opened her chelicerae and bit into the male's cheliceral groove lying between the two cheliceral apophyses. Her fangs remained firmly between these cheliceral apophyses (Fig. 8). During cheliceral clasping, the male performed rough up-and-down movements. Hinge-like body movements were performed 3-7 times, while pulling the female backwards. If the female was small or showed low resistance, the male pulled the female out of the retreat and copulation took place on the sheet-web. Otherwise, the male pulled the female to near the entrance. The duration from

beginning contact with the female to the completion of clasping varied from 10 sec to 8.5 minutes.

Copulation.—Twenty-six copulations were observed. Copulation can occur completely inside the retreat. Cheliceral clasping and the long male palps allowed a non-elevated copulation position, which took place in the narrow silk tube. The ventral angle between longitudinal body axes was 90° (if male is small) or more. Also, the cephalothorax and abdomen can adopt a small dorsal angle to facilitate mating in small spaces. Females were extremely passive during copulation. However, when one copulating male was intentionally disturbed for photographic purposes, the female attacked and killed him. Later the same

day, the same female copulated normally with another male. In another encounter, the couple had difficulty in uncoupling: the male remained entangled in the web after being released. The female then attacked and killed him.

During copulation (Fig. 9), the male-female ventral body angle varied (according to spider size) between 90–130°. The female's legs I and II were flexed against her body. The male placed his forelegs dorsally on the female, legs II more laterally, with legs III and IV on the floor, maintaining the equilibrium. Male palps were extended to the female venter during copulation (Fig. 9). That the male palpal femora and tibiae are bent dorsally was evident during insertion.

The palpal insertion pattern was complex. The embolus reached a perpendicular position with respect to the dorsum of the palp, but turned slightly back to be inserted (Fig. 10). Embolus movement was reconstructed in dead specimens under the stereo-microscope. The palpal bulb rotated around an approximately dorso-ventral axis of the palpal tarsus. The palpal embolus emerged retrolaterally, moving along the glabrous notch and stopping in a small retrolateral lobe (see Gertsch & Platnick 1979, figs. 46, 47, 50). Palpal bulb rotation was complex. Initially the tip of the embolus turned retrolaterally and later went upward; it is possible that the whole palp also rotates. When manipulated in preserved specimens, the embolus is flexible. In resting position the palpal embolus is prolateral and parallel to the longitudinal axis of the palpal tarsus, its tip points forward, and it is protected by a wide notch and a prolateral paracymbium-like lobe.

During copulation the palpal tarsus approached the epigastric furrow, which appeared swollen. The embolus was inserted and, in this position, insertion/withdrawal movements were repeated numerous times. These movements were generated by the tibio-tarsal joint of the palp. Withdrawal movements were discontinuous, suggesting that they must overcome a mechanical resistance. Discontinuous female abdominal movements were also observed synchronously. During withdrawal movements the palpal tarsus reached a dorsal angle of nearly 90° with respect to the tibia. Finally, the palp remained immobile in the insertion position. Only the

corkscrew-shaped portion of the embolus penetrated during insertion, the straight basal portion remained visible. We attempted to reconstruct the insertion with dead specimens and observed that only the right embolus can enter the right receptacle (and the same for left organs) according to the complementary spiral orientation. During the insertion of one palp the other remained extended, either moving or being immobile against the female abdomen. The embolus extraction was similar to insertion-withdrawal movements, pivoting on tibio-palpal joint. Despite the difficult observation of small spiders through the dense webs, the insertion pattern was clearly seen in 12 copulations and partially observed in another 4.

During early palpal insertions, the in-out movements were frequent. Males performed three, four, five or more insertion-withdrawal movements during a period of 1–6 min. The palps did not always alternate; two–four successive insertions with the same palp were common, especially following a failed insertion attempt.

Males performed 2–22 ($\bar{x} = 10.3 \pm 6.5$, $n = 10$) palpal insertions during a period of 5.7–30.0 min ($\bar{x} = 18.4 \pm 8.6$ min). Late insertions were brief (10–40 sec) and involve in-out movements only during palpal extraction. Other behaviors present in the periods between insertion attempts increased in frequency during the later stages of copulation. These behaviors were: pulling of male and female, moving outside and inside the retreat; rearrangement of legs; hinge-like movements (when the angle between the bodies changes); leg push from male to female, etc.

During the 26 copulations observed, only two pairs reclasped after unclasping. Unclasping had complications. The male pulled and/or pushed the female, forcing her outside the retreat and pulling her with his legs. The most conspicuous maneuvers of the male were cheliceral outspreading as well as series of violent hinge-like movements. The female allowed unclasping and determined the end of the copulation. When females did not release the male chelicerae, additional insertions could occur. An extreme case was a male which attempted to unclasp after 35 min of copulation but the female kept him in the copulation position for 21.5 min more. In another remarkable case the female dragged along the

male (for 32 min) because one fang remained clasped. This long interaction ended when the male unclasped (at 120 min) and the female killed him. Chelicer anomalies were not found in these specimens.

Copulation duration from the start of clasping to complete unclasping was 11–56.5 min ($\bar{x} = 24.7 \pm 10.0$, $n = 23$). Three other copulations were unusual. Two of these pairs unclasped and clasped again: one unclasped at 19 min, clasped again after 3 min and continued copulating for 18 min; the other unclasped at 14.5 min, clasped again after 3 min and then definitively unclasped without inserting, after 2 min. The third case was described above and involved the most difficult unclasping, which lasted 88 min.

All available individuals in the laboratory copulated (18♂, 13♀). In some cases copulation did not occur during the first encounter, but only after a second (two cases) or third attempt (one case). Failed attempts were one with a virgin female and three with once-mated females. Eight males recopulated between 8–47 days after first copulation. Twelve females (one female died after first copulation) recopulated between 5–44 days after first copulation; one female made a third copulation 12 days after the second copulation.

Postcopulatory activities.—Thirteen males were very active after copulation. These activities included leg tapping, violent pushes with outspread chelicerae, and conspicuous body vibrations when males pursued females. Females hid in the retreat and remained very passive. In response to these male behaviors, females flexed their legs against the body and remained immobile (with venter up in two cases). These males continued pursuing the female until the female abandoned her web. If the female returned, the male pursued her again until she remained outside the web. These males then took over the female webs, occupying the retreat. In other cases the males touched the female, made palpal drumming and slightly pushed her. In four encounters the male remained peacefully in the retreat with the female for 30 min, at which time he was removed. In three encounters the female left the web and came back several times, without being disturbed by the male. In another three encounters, males ran away from the web after copulation. Finally, in two encounters both partners ran away after copulation and in one

encounter the female killed the male after a difficult uncoupling.

In four encounters carried out in Arena B, with a more complex web, the female retreated to the bottom of the funnel. Although the males persisted, only one female left the web. In the other three encounters the male stayed together with the female for at least 30 min. These males placed themselves at the entrance of the funnel web and sporadically contacted the female; but no attacks were observed. Later, another male (intruder) was placed in each of these three webs which the males were guarding. These intruders began to court as soon as they touched the web near the entrance. Then the guarding male vigorously attacked the intruder. In one case the intruder won; the guarding males won the other two contests. In one of these last two encounters the fight was long; the males fought in a ritualized manner, pushing themselves with outspread chelicerae, which resemble a rhomboid from the dorsal view. With legs I and II firmly interlaced, the males bit the web several times. After a separation, one male caught the other from behind but did not bite him; when the first turned around they re-initiated the frontal embrace. Guarding winners touched the females and returned to guarding. The intruder winner unsuccessfully courted the female. No spiders were damaged. Males were removed between 30–60 min after copulation.

Two other copulations, one partially recorded in a Super-8 movie-film, were observed in 1990, using Arena A. Courtships and copulations were similar to those previously described and copulation durations were 24.5 and 55 min.

DISCUSSION

Habitat and webs.—The high sensitivity of *M. thorelli* to humidity variations seems to be critical in understanding its biology and ecology. In the laboratory, individuals not provided with abundant water quickly died, but a minimal excess of water also caused the death. This sensitivity clearly suggests a high dependence on the funnel-and-sheet web. The need for hygro-thermo stability is also emphasized by reinforced by their habit of living under stones, roots and trunks, in hilly areas in streamside forests. Probably the web gives protection from desiccation and occasional flooding. Although this species lives near the

water it does not invade the stones of the dry stream bed (Costa et al. 1991; Pérez-Miles et al. 1993). Then, *M. thorelli* seems to be very restrictive in its habitat selection. Collection data from Argentina, Provincia de Buenos Aires, generally agree with our findings (Holmberg 1882; Goloboff & Ramírez 1991; Maury *in litt.*). Also, North American Mecicobothriidae live under stones or other objects in the soil, in crevices, and deep in organic ground litter (Gertsch & Platnick 1979). These species are frequently found in the shade of coniferous and oak woods from Washington and Oregon to California (western USA).

Our observations indicate that adult males do not construct funnel-and-sheet webs, but Holmberg (1882) found the holotype male in a funnel web of 2 cm length which opened onto a sheet of 2 cm². Holmberg was not sure if the male was occupying its own web because he found several individuals of "*Teegenaria*" in coexistence. *M. thorelli* found in Sierra de las Animas were syntopic with hydrophilic spiders of the genus *Diapontia* (Lycosidae), the webs of which could correspond to Holmberg's "*Tegenaria*". However, it is more likely that the male collected by Holmberg was occupying a conspecific female web; this would fit our observations of post-copulatory female expulsion. Or perhaps this male had recently molted to adulthood in his juvenile web.

Apart from the role of webs in water regulation, they also play a key role in prey capture. *M. thorelli* has long posterior spinnerets well suited for sheet-web construction and repair. Biting and pulling back behavior in prey capture is widely distributed among spider taxa, suggesting a primitive condition. This technique is simple and safe because entangled threads effectively prevent the defensive movements of the prey. North American Mecicobothriidae also live in funnel-and-sheet webs and show similar prey capture tactics (Gertsch & Platnick 1979).

Life cycle.—Most spiders collected in September 1994 molted in October 1994 (Fig. 4). This synchronized development would reflect the influence of uniform breeding conditions, mainly feeding. These juveniles molted 2, 3 or 4 times to reach maturity. Therefore, maturity molting seems to occur in a fixed period of the year, independent of the initial developmental stage. Two main factors seem to de-

termine the time when the spider will molt to maturity: biorhythm and seasonal environmental factors. Females reach maturity before males, which explains why males molt more times than females during September–April. Females of *Hypochilus pococki* Platnick 1987 (Hypochilidae) also reach maturity earlier than males (Catley 1993).

The results suggest that maturity molting and sexual activity occur at the beginning of the cool period, which is also supported by the collection dates of Holmberg (1882), Gertsch & Platnick (1979) and Pérez-Miles et al. (1993). In the field Pérez-Miles et al. (1993) found adult males from May to September, with a peak of activity in July. These authors interpreted the fall/winter activity as a way to avoid predation. We also interpreted the synchronized male maturity in the same way, satiating the scarce winter predators. A capture of a male in October in Sierra de la Ventana, Argentina (Gertsch & Platnick 1979) seems to be extremely late. However, several captive males remained alive during September and a few in October, suggesting a longer lifespan in the laboratory. The male activity period of *M. thorelli* resembles a "stenochronous, winter-mature species" of Schaefer (1987), a category mainly occupied by Linyphiidae in Europe. However, this species has a longer lifespan – at least three years. Individuals molt more than expected for their size and have two periods without molting (winter and summer). The wide range of sizes found in field samples and laboratory developmental data suggest the coexistence of at least three generations.

Reproduction.—As far as we know, our observations of the sexual behavior of *M. thorelli* are the first ever published for any species of Mecicobothriidae. Females of *M. thorelli* may release a sex pheromone, which has previously been reported for Mesothelae (Haupt 1977) and several families of Mygalomorphae: Antrodiaetidae (Coyle & Icenogle 1994), Atypidae (Coyle & Shear 1981), Dipluridae (Coyle 1985, 1986b), Nemesiidae (Buchli 1962; Costa 1982) and Theraphosidae (Baerg 1958; Minch 1979; Pérez-Miles & Costa 1992). This wide distribution indicates that tactochemical sexual communication is an early acquisition in spiders. The effect of a sexual pheromone of *M. thorelli* should be of short duration and/or it would only be released

near the retreat, considering that males started the courtship in the sheet web.

Courtship characteristics suggest that vibrations transmitted through the silk threads are the primary means of communication before direct contact. Male sexual behavior strongly inhibited female attacks. The extreme passivity of females during courtship, copulation and postcopulation is remarkable, although it is common in mygalomorphs (Jackson & Pollard 1990). Only if we manipulated a couple during copulation was the male attacked and cannibalized.

Cheliceral sexual clasping has been reported in Mygalomorphae only for *Atypoides riversi* O.P.-Cambridge 1883 (Antrodiaetidae; Coyle 1971) but not involving fang clasping as in *M. thorelli*. However, it resembles that of some Araneomorphae. For example, in some species of *Pachygnatha* Sundevall 1923 and *Tetragnatha* Latreille 1804 (Tetragnathidae) males immobilize female chelicerae with their own modified chelicerae (Bristowe 1941). Also males of *Hypomma bituberculatum* (Wider 1834) (Linyphiidae) (Bristowe 1931, 1941) and *Argyrodes antipodiana* (O.P.-Cambridge 1880) (Theridiidae) (Whitehouse 1987) immobilize female chelicerae by stimulating female biting on male frontal tubercles. In Theraphosidae, precopulatory and copulatory female clasping on tibial spurs of male forelegs is a well-known mechanism (Baerg 1928, 1958; Minch 1979; Pérez-Miles & Costa 1992). The sexual embrace, behavior and reproduction of Mygalomorphae were reviewed by Coyle (1985, 1986b), Coyle & O'Shields (1990), Jackson & Pollard (1990) and Costa & Pérez-Miles (1992).

The male of *M. thorelli* elicits female clasping by pushing her with his chelicerae repeatedly. The cheliceral embrace is a *sine qua non* condition for a successful copulation. Female biting appears to cancel the aggressive and/or predatory impulse and consequently inhibit further attacks. In *Alopecosa cuneata* (Clerck 1757) (Lycosidae), where males offer their incassate foreleg tibiae for female biting (Kronstedt 1979, 1990) a similar explanation could be applied. The release of aphrodisiac pheromones from these male structures was also suggested (Kronstedt 1986; Whitehouse 1987).

In Mecicobothriidae, cheliceral clasping is only present in *M. thorelli*. In *Megahexura*

Kaston 1972 and *Hexura* Simon 1884, males have a series of short spines above the chelicerae, distally stronger (Gertsch & Platnick 1979), suggesting their use in copulation. These structures may perform a similar to that found in *Atypoides riversi* (Antrodiaetidae). Coyle (1971) observed that in this species the males used their long cheliceral apophyses to hold the outspread female chelicerae during copulation. Clasping of *M. thorelli* might have evolved from a frontal fight with full contact of chelicerae, common in agonistic encounters. In successive steps male chelicerae would be modified to neutralize female biting and increase male security during copulation. Clasping also serves in communication and epigamic sexual selection, as well as to hold female in position (Coyle 1985, 1986b; Eberhard 1985; Jackson & Pollard 1990).

In its initial stages cheliceral clasping requires very complex movements. Positional reconstruction with dead specimens helped us understand the mechanics of clasping. We were able to verify that: 1) Both male and female must separate the basal segments of the chelicerae laterally; 2) Females must fully open the cheliceral fangs obliquely; 3) The introduction of the female fangs is initially divergent and finally convergent; 4) Female fangs enter the male cheliceral channels up to the basal incassate region. Male hinge-like movements facilitate this rigid clasping position; 5) In *copula*, the basal chelicerae of female and male remain closed; 6) Two simultaneous procedures are necessary for unclasping: male cheliceral opening with hinge-like movements, and female cheliceral opening with fangs relaxed; 7) Males must move downward and the female upward.

Male safety during copulation is reinforced by positioning the forelegs on the female, which probably prevents the female from biting the male prosoma. The long palps of the male allow him to copulate more horizontally than other mygalomorphs. Consequently, mating can take place safely inside the retreat. Also, male backward movements probably improve clasping.

Copulation of *M. thorelli* is very complex and long in comparison with other mygalomorph spiders. The insertion/withdrawal palpal movements deserve special attention. The palpal embolus is rigid and spiral-shaped and cannot enter by rotation as in other araneo-

morphs or *Latrodectus* (Abalos & Báez 1967; Grasshoff 1973). The palpal embolus must enter forcibly, spiral by spiral, in a discontinuous jerky movement which would explain the female's sudden movements. This penetration appears to be made possible by the elasticity of the embolus, as well as the spermathecae. The number of embolus spirals and spermathecae spirals are the same – four. This close correspondence suggests that the whole embolus enters the inner spiral-shaped receptacle but not in the outer round receptacles (see fig. 38 in Gertsch & Platnick 1979). This unique penetration pattern probably causes intense genitalic stimulation which would determine sexual selection by female choice, following Eberhard's theory (Eberhard 1985). This stimulation might also have an inhibitory function on non-sexual female behaviors.

The characteristics of both embolus and receptacle spirals require that the palpal insertions must be crossed (right palp in right receptacle, and left palp in left receptacle). This crossed insertion is the norm in araneomorphs but has not been indicated yet for the mygalomorphs. Although the insertion mode is not evident from direct observation, it was confirmed from the study of helicoidal orientation complementarity between male and female genitalia. The orientation of both embolus tips and receptacle basis would also suggest that only crossed palpal insertion is possible. The wide separation between receptacle bases would facilitate a correct insertion.

Male postcopulatory behavior in *M. thorelli* is remarkable. Some males seemed to practice postcopulatory mate guarding, which would be predicted on the basis of this species spermathecal morphology (cul-de-sac type of Austad 1984). Mate guarding prevents later copulations with other males and consequently sperm competition, but can be only maintained for a brief time. Although the morphology of the receptacle stalk is adequate for mating plugs, males recopulated normally, which suggests the absence of mate plugs in *M. thorelli*.

Unlike mate guarding, female expulsion is an uncommon male postcopulatory behavior in spiders, and without a clear interpretation in *M. thorelli*. Isolated males may have an excessive aggressive motivation due to the absence of fights in natural male-male encounters. Another factor would be the fragmentary

webs constructed by females in the laboratory; these would facilitate female expulsion. In the laboratory, females with deep retreats were less likely to be expelled than were those with shallow retreats; in the field deep retreats were the only type observed. However, high female tolerance to males seems to be a species-specific tactic which could be understood if combined with cryptic female location.

In the laboratory, copulated females did not spin intensely in winter and they dug deeply into the soil. Usually they did not make an exterior sheet for prey capture, and therefore would not be found by males (nor collectors). This cryptic postcopulatory female behavior, together with female expulsion by the male, could protect the paternity of the copulating male. Our hypothesis agrees with the high competition expected among males of *M. thorelli* which reach maturity synchronously and have an activity peak in July (Pérez-Miles et al. 1993).

At first, our hypothesis fails to explain the benefits from the female perspective because she loses her web and, consequently, the possibility of other copulations. New copulations would increase the variation of her offspring and avoid the risk of a single copulation with an sterile male. (See Austad 1984 for a review of remating advantages for females). However, some female benefits could be suggested.

If prey were scarce in winter, it would be more economical for a female to suspend predation and thereby avoid the cost of web maintenance, predation and parasitism risks, considering the low metabolic rates of the spider in this season. The risk to the female during expulsion from the retreat would be minimal if a low predation level in winter is assumed (Pérez-Miles et al. 1993). Webs could elicit persistent courting males which make prey capture difficult and also attract predators. This would help to explain the "complicity" of the female in allowing the weak male to expel her. Two field observations are consistent with the hypothesis: 1) we did not find adult females in September, when intense collections were carried on, and 2) a male found by Holmberg in 1881 was probably occupying a web of an expelled female.

M. thorelli make eggsacs earlier (at the end of winter and end of spring) than North American Mecicobothriidae (spring and summer) (Gertsch & Platnick 1979). The eggsacs of

these species are round as in *M. thorelli*, except in *Hexura rothi* Gertsch & Platnick 1979 (lenticular). The number of eggs is related to spider size: *M. thorelli* (body length approximately 7 mm) laid between 23–33 eggs; *Hexura rothi* (body length approximately 11 mm) laid 80 eggs, *Hexurella* Gertsch & Platnick 1979 species (body length between 3–4 mm) laid only 4–7 eggs (Gertsch & Platnick 1979).

Phylogeny and biogeography.—The monophyly of Mecicobothriidae, supported by Gertsch & Platnick (1979), Raven (1985) and Goloboff (1993), is considered as a starting point to discuss some biogeographical aspects. The amphitropical distribution of the Mecicobothriidae is similar to that reported to some coleopterans, fishes and plants (Humphries & Parenti, 1986). According to Gertsch & Platnick (1979) and Raven (1985), *Hexurella* seems to be the sister genus of the rest of Mecicobothriidae and consequently *Mecicobothrium* is more closely related to the mecicobothriid genera *Megahexura* and *Hexura* than to *Hexurella*. Considering the present geographic distribution of these taxa, only an ancient generic cladogenesis (pangeic) could be hypothesized, prior to the separation of the Americas. Avoiding dispersalist interpretations, a post-pangeic cladogenesis of North American genera could only be proposed if *Mecicobothrium* was the sister genus of the rest of Mecicobothriidae.

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